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ORIGINAL ARTICLE

Underuse of stopover site by migratory swans

Bart A. Nolet · Abel Gyimesi

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Abstract Many migratory birds use a chain of stopover sites to fuel their migration. Under time-minimizing migration, fuelling time and giving-up density at stopovers are predicted to depend on fuelling conditions. Fluctuations in food accessibility likely lead to changes in fuelling conditions, which should in turn be reflected in fuelling time and giving-up density. During their migration, Bewick's Swans *Cygnus columbianus bewickii* refuel on below-ground tubers of Fennel Pondweed *Potamogeton pectinatus* in shallow lakes. We studied giving-up density and stopover use (expressed in bird-days) of Bewick's Swans at an autumn stopover site (Lauwersmeer, The Netherlands) during 1995–2008, as dependent on local environmental conditions. High water levels were hypothesized to restrict access to tuber stocks. High water levels at the stopover site were predicted to lead to higher giving-up densities and less bird-days spent at the stopover. Annual variation in giving-up densities and number of bird-days was strongly associated with year-to-year differences in initial tuber biomass density and number of days with high water levels. As predicted, giving-up density increased and bird-days decreased with the number of days with high water level. We conclude that, in line with time-minimizing migration, changes in fuelling conditions may lead to underuse of a stopover site. Underuse of stopovers by migratory birds has been reported before but only in the sense that more food was left at stopover sites than at wintering sites. In contrast, in our case, dealing with a given stopover site, more food is left behind in some years than in other years.

Keywords Bewick's Swan · Food availability · Migratory fuelling · Time-minimizing migration · Staging site · Water level

Zusammenfassung

Unternutzung eines Rastplatzes durch Schwäne

Viele Zugvögel nutzen aufeinanderfolgende Rastplätze, um Energie für ihren Zug aufzunehmen. Um die Zugdauer zu minimieren, sollte deshalb die „Auftankzeit" und die Nahrungsdichte beim Verlassen eines Rastplatzes („Aufgabedichte") von den örtlichen Auftank-Bedingungen abhängen. Fluktuationen in der Nahrungserreichbarkeit können zu Änderungen in diesen Auftankbedingungen führen und sollten sich in Auftankzeit und Aufgabedichte niederschlagen. Singschwäne *Cygnus columbianus bewickii* ernähren sich während ihres Zuges von Wurzelknollen des Kammlaichkrauts *Potamogeton pectinatus* im Flachwasserbereich. Wir untersuchten die Nahrungsaufgabedichte un die Rastplaztnutzung (gemessen in Vogel-Tagen) von Singschwänen und deren Abhängigkeit von den lokalen Umweltbedingungen an einem Herbstrastplatz in den Jahren 1995–2008. Hohe Wasserstände sollten den Zugang zu den Wurzelknollen begrenzen und damit zu höheren Nahrungsaufgabedichten und einer geringeren Anzahl an Vogel-Tagen auf diesem Rastplatz führen. Die jährlichen Variationen in den Nahrungsaufgabedichten und den Anzahlen an Vogeltagen waren stark mit Unterschieden in der

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B. A. Nolet (✉)
Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, The Netherlands
e-mail: b.nolet@nioo.knaw.nl

A. Gyimesi
Department of Bird Ecology, Bureau Waardenburg, Varkensmarkt 9, 4101 CK Culemborg, The Netherlands

Wurzelknollendichte bei Ankunft am Rastplatz sowie der Anzahl der Tage mit hohen Wasserständen verbunden. Mit der Anzahl an Hochwassertagen erhöhte sich, wie erwartet, die Nahrungsaufgabedichte und verringerte sich die Anzahl der Vogeltage. In Übereinstimmung mit den Vorhersagen zur Minimierung der Zugdauer schlussfolgern wir, dass Änderungen in den Auftankbedingungen zu einer Unternutzung von Rastplätzen führen können. Solche Unternutzungen von Rastplätzen waren zwar bereits berichtet worden, doch nur insofern, dass an den Rastplätzen mehr Nahrung zurückblieb als an den Winterplätzen. Wir dagegen zeigen, dass die nicht genutzte Nahrung innerhalb eines Rastplatzes von Jahr zu Jahr schwanken kann.

Introduction

Many migratory birds use stopover sites where they fuel for migration (Alerstam and Hedenström 1998). During migration, more time is commonly spent on stopovers than travelling, particularly in birds using flapping flight (Hedenström and Alerstam 1997). Hence, stopover duration largely determines migration speed.

Theory predicts that time-minimizing migrants should stay at a stopover as long as the rate of increase in body fuel enables a faster migration than the overall migration speed on their journey (Alerstam 1991; Alerstam and Lindström 1990). In flying animals, fuel load comes with a flight cost (Pennycuick 1975; Kvist et al. 2001), and therefore potential flight range, and hence migration speed, is expected to increase at a decelerating rate with fuel load (Alerstam 1991; Alerstam and Lindström 1990). Because fuel load is supposed to increase with fuelling time, diminishing returns of potential flight range are expected with increasing fuelling time (Alerstam and Hedenström 1998). At the stopover, carrying and maintaining a given fuel load already comes at a cost, and this will further slow down the increase in flight range with fuelling time (Klaassen and Lindström 1996). Moreover, food depletion might cause diminishing returns of potential flight range with fuelling time, because depletion often leads to lower fuelling rates (Nolet and Drent 1998; but see Lourenço et al. 2010). Together, fuel load and food depletion determine the optimal fuelling time at a stopover (Alerstam and Lindström 1990; Alerstam 1991). If conditions are unfavourable at a particular stopover site, migrants have been shown to move on (Newton 2006, and references therein) and to depart with low fuel loads, as expected when migrants aim to migrate as fast as possible (Lindström and Alerstam 1992).

The main factors determining the fuelling conditions (and hence fuelling time or stopover duration) of a stopover site are its food abundance (Newton 2006), the costs of harvesting that food (Van Eerden et al. 1997b) and food accessibility (Zwarts et al. 1992). Predation risk also affects site use, in particular for small to medium-sized birds, and is often traded-off against food availability (Clark and Butler 1999; Guillemain et al. 2007; Pomeroy et al. 2006; Duijns et al. 2009; Cresswell 1994). These are also the factors known to affect giving-up densities (GUDs), i.e., the food densities remaining after animals have left a food patch (Brown 1988; Nolet et al. 2006a). Hence, GUDs at a stopover site have been proposed to reflect the long-term fuelling rates along the migration route (Van Gils and Tijsen 2007).

Bewick's Swans *Cygnus columbianus bewickii* (Yarrell) fuel their migration by feeding on aquatic macrophytes, especially tubers of Fennel Pondweed *Potamogeton pectinatus* (Beekman et al. 1991; Nolet et al. 2001a, b). During aquatic foraging of these large birds (c. 6.0 kg), predation risk can be neglected, which partly explains why they prefer to forage on water over field feeding (Nolet et al. 2002). For instance, the largest avian predator in their aquatic habitat, the White-tailed Eagle *Haliaeetus albicilla*, only exceptionally takes birds of more than 2.5 kg (Cramp and Simmons 1979). Therefore, aquatically foraging Bewick's Swans are well suited to study the effects of fuelling conditions on stopover use without the confounding effects of predation risk.

In waterbirds, fuelling conditions may be affected by water depth (De Leeuw et al. 1998; Lovvorn 1994; Guillemain et al. 2000; Gawlik 2002). In Lauwersmeer, an important autumn staging site of Bewick's Swans in the Netherlands, within-year (i.e., spatial) variation in GUD was related to water depth (Nolet et al. 2001b), largely due to differences in food accessibility and to a much lesser extent by differences in foraging costs (Nolet et al. 2006a). Because accessibility is directly influenced by water levels, we hypothesize that inter-annual (i.e., temporal) variation in GUD at the stopover site is related to yearly differences in initial food density *and* water level. As the difference between initial and final biomass represents the biomass consumed by swans (Nolet et al. 2006b), both the initial food density and water levels should also influence stopover duration (at the individual or population level). Hence, we predict that lower food accessibility leads to shorter stopover duration and higher GUDs (Fig. 1). Effectively, this would result in the underuse of the stopover site in some years, in the sense that food is left unexploited, because it was (temporarily) inaccessible.

Methods

Study area

Lauwersmeer is a shallow freshwater lake (2,400 ha, water volume 0.05 km^3) formed by damming of a bay of the

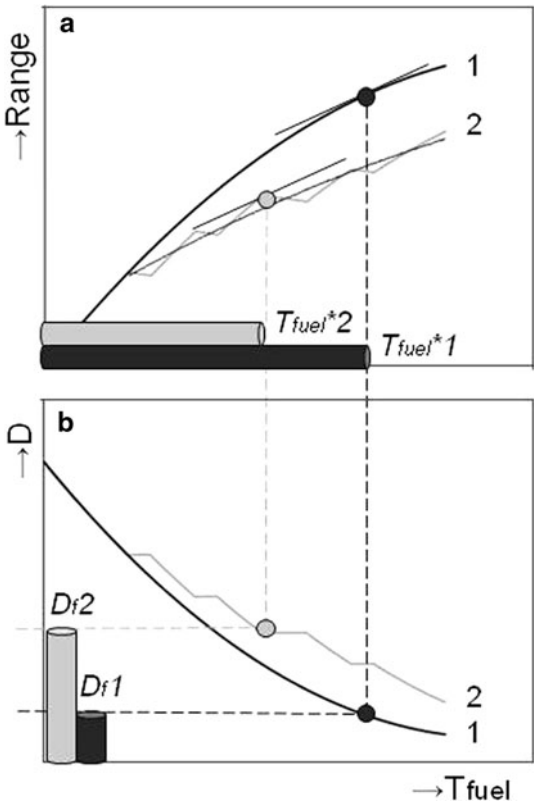

Fig. 1 Optimal fuelling time at a stopover and corresponding giving-up density according to optimal bird migration theory. **a** In migratory birds, potential flight range to the next stopover is expected to increase with fuelling time (*Tfuel*) at the current stopover, but with diminishing returns (see text). Birds are expected to leave a stopover site when the marginal value (*tangents*) of flight range on fuelling time falls to their expectation for the whole migration (indicated by *dots*). A reduction in fuelling conditions leads to a slower increase in flight range (*grey curve*), and hence an earlier departure. Optimal stopover duration (*Tfuel**) is predicted to be longer under standard (*1 horizontal black bar*) than under reduced (*2 grey*) fuelling conditions. **b** Due to depletion, food density (*D*) at the stopover is expected to decrease with fuelling time (*Tfuel*), at an increasing rate when more birds settle at the stopover site. A reduction in fuelling conditions leads to a lower depletion rate (*grey curve*) and a higher giving-up density (D_f; *2 grey vertical bar*) than under standard conditions (*1 black bar*)

Wadden Sea in 1969, and recharged by two small rivers. Water levels are strictly regulated, although rapid changes in water level can occur, depending on rainfall, wind direction and state of the tide in the Wadden Sea (determining whether water can be sluiced). Our study site was an inlet (Babbelaar) closed to the public.

Tuber sampling

Tubers were sampled along the north-east shore (53°20′27″N, 6°13′43″E) of the inlet between 1995 and 2008. Initially (1995–1998), we sampled in three 20 × 20 m plots 100 m apart (plots 11–13 in fig. 1 of Nolet et al. 2001b). In 1995, we took 18 sediment cores per plot (54 cores in total), but in 1996–1998 we doubled this number (i.e., 36 cores per plot, 108 in total). In later years (2001–2008), we sampled the same area in a grid of 200 × 40 m with 1-m^2 sampling points 20 m apart, taking 12 cores per point (396 cores in total). The 20-m distance between sampling points was sufficient to prevent spatial autocorrelation (Nolet and Mooij 2002). Cores were 10 cm in diameter and >30 cm deep. These were washed over a 3-mm sieve to collect the tubers, which were taken to the laboratory, dried for 48 h at 70 °C, and weighed (all weights refer to dry weight).

Samples were taken in late September or early October, just before the swans arrived, to assess initial tuber biomass density D_i. After the swans had left, usually by mid-November, samples were taken to assess the giving-up tuber biomass density D_f. In March, shortly before sprouting of the tubers, samples were taken to determine the tuber biomass density left after the winter D_s. Sampling plots and points were marked with small bamboo sticks 10 cm above the sediment, well below the water surface, to enable re-sampling at the same locations. From 2001 onwards, we sampled the same exact 1 m^2, so for these years we corrected the initial tuber density by subtracting the sampled area (12 π 0.05^2 m^2; i.e., close to 10 % of plot area) times D_i (i.e., $D_{ic} = 0.91\ D_i$). In the earlier years, sampled area was <1 % of plot area, and such a correction was ignored.

Swan observations

With the aid of 20–60× telescopes, Bewick's Swans in the inlet were counted daily from the day the first swans arrived until they had all switched to surrounding arable fields or continued southward migration. Daily numbers were summed to obtain the number of swan-days, *S*, per year, linearly interpolating numbers on missing days (comprising 8.6 % of the total *S*).

Water levels

Water levels in Lauwersmeer, obtained from Waterschap Noorderzijlvest, were expressed relative to the Dutch standard (NAP). Daily mean water levels measured at two stations (Zoutkamp, 53°20′14″N, 6°17′49″E; Nieuwe Robbengat, 53°23′28″N, 6°14′12″E) either side of the Babbelaar were averaged. The distribution of average daily water levels in October–November was right skewed (Fig. 2; Skew = 1.81 ± 0.08 SE, Shapiro–Wilk $W = 0.805$, $P < 0.001$), reflecting rapid peaks in water level rise. Rather than using average daily water level, we calculated the number of days with "high" water levels *h* (i.e., higher than the critical water level) as our independent variable. As the critical water level, we took the mean of

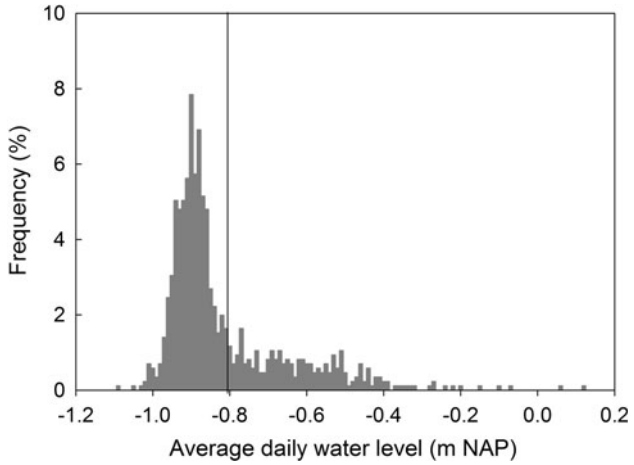

Fig. 2 Frequency distribution of daily water level in Lauwersmeer (average of two stations) in October–November 1995–2008 ($n = 854$); water level aimed for by the water board is −0.93 m NAP (NAP = Amsterdam Ordnance Datum, data Waterschap Noorderzijlvest). *Vertical line* indicates mean value of −0.81 m NAP

the observed water levels (−0.81 m NAP), but any critical level between −0.83 and −0.68 m NAP yielded similar results (not shown).

Statistics

Variables were tested for normality with Shapiro–Wilk W test. We compared 7 models of final tuber density D_f and swan-days S, respectively, as functions of initial tuber density D_i (or corrected initial tuber density D_{ic} in the case of D_f), days with high water h, and their two-way interactions, in all possible combinations. Akaike's information criterion corrected for small sample size was used to select the most parsimonious model in this model set (Burnham and Anderson 2002). Because the order of models is to some extent dependent on the measurement scale of the variables when including an interaction term, we first normalized all variables x to x_{norm} ($0 \leq x_{norm} \leq 1$) by taking $x_{norm} = (x - x_{min})/(x_{max} - x_{min})$, where x_{min} and x_{max} are the minimum and maximum values of a variable, respectively. We regarded D_f to be a function of local D_i, hence our choice for D_{ic} when modelling D_f. S, however, was regarded to be a function of a more global D_i.

Swan usage and realized final tuber density were predicted from initial tuber density and days with high (i.e., above-average) water levels as follows. As the functional response is nearly linear (Nolet et al. 2002), the foraging time at $h = 0$, indicated by $t(0)$, to deplete a unit area to $D_f(0)$ can be approximated as:

$$t(0) = (1/(a \cdot \varphi)) \cdot \ln(D_i/D_f(0)),$$

where a is the attack rate, and φ is the proportion of foraging time spent feeding (feeding by head-dipping or up-ending is part of foraging which also includes digging and breathing pauses). As values, we took the average for sandy and clayey sediments, as both occur in the inlet, giving $\varphi = 0.74$ and $a = 0.00082$ m^2/s (Nolet and Klaassen 2009). We assumed that the effective foraging time linearly decreases with the number of days with above average water levels ($0 \leq h \leq 61$):

$$t(h) = t(0) - h/61 \times t(0)$$

The number of swan-days at h days with above average water levels $S(h)$ is then:

$$S(h) = (t(h) \cdot A)/(24 \times 60 \times 60),$$

where A is the area of pondweed in the inlet (17.7×10^4 m^2) (Nolet et al. 2006b). Realized final tuber density $D_f(h)$ is obtained after re-arranging:

$$t(h) = (1/(a \cdot \varphi)) \cdot \ln(D_i/D_f(h)),$$

which yields:

$$D_f(h) = \exp(\ln D_i - a \cdot \varphi \cdot t(h)).$$

Results

In Lauwersmeer, final tuber density D_f increased with the (corrected) initial tuber density D_{ic} (Table 1, model 3) and number of days with above average water levels h (Table 1, model 2), both variables explaining the final tuber density equally well. The most parsimonious model included both these variables, such that D_f increased with D_{ic} depending on the number of days with above average water levels h (Fig. 3a). This could explain the exceptionally high D_f in 2006 (highest data point in Fig. 3a), when there were many days of above average water levels in Lauwersmeer ($h = 36$).

There was little difference in empirical support between the two top models predicting swan-days S, both including the initial tuber density D_i and the number of days with above average water levels h (Table 2, models 1–2). In general, S increased with D_i and decreased with h, and these models only differed in the way the number of days with above average water levels h changed the relationship between S and D_i (i.e., running parallel or divergent; the latter is shown).

Using the experimentally derived functional responses yielded very similar patterns of final tuber density (Fig. 3b) and swan usage (Fig. 4b) as the depicted statistical relationships (Figs. 3a, Fig. 4a).

The reduction in tuber biomass from November to March (17.8 % ± 6.1 SE, $n = 11$), after the swans had left Lauwersmeer, was not significantly different ($t_{10} = -1.85$, $P > 0.09$) from winter mortality without swan grazing (6.5 %, assessed using winter exclosures) (Hidding et al.

Table 1 Top 3 explanatory models to explain final tuber density D_f in Lauwersmeer in 1995–2008 according to Akaike's information criterion corrected for small sample size (AICc; $n = 11$)

Model	K	Deviance ratio	ΔAICc	$L(m_i\|x)$	w_i	Evidence ratio	RMSD (g/m^2)	r^2
1. $\boldsymbol{D_{ic} \times h}$	**3**	**14.0**	**0.00**	**1.00**	**0.53**	**1.0**	**3.38**	**0.61**
2. h	3	18.6	2.41	0.30	0.16	3.3	3.90	0.48
3. D_{ic}	3	19.7	3.05	0.22	0.11	4.6	4.02	0.45

Each model is defined by the listed independent variables: corrected initial tuber density D_{ic}, number of days with above-average water levels h, and possible interaction terms (×). All models with substantial empirical support (i.e., ΔAICc < 2) are indicated in bold; K is the number of parameters, $L(m_i|x)$ is likelihood of model i given the data, and w_i is its Akaike's weight (Burnham and Anderson 2002). RMSD is the root mean squared deviation of observed on predicted values of (in this case) D_f, and r^2 the coefficient of determination (i.e., proportion of the variation in observed values explained by the predicted values of, in this case, D_f)

2012) (Fig. 5). Only in 1996 was a relatively large reduction (63 %) measured (Fig. 5; light grey point well below the line).

Discussion

Swans left more tuber biomass at the stopover site when more days with high water levels occurred. In a previous analysis, the positive relationship between initial (D_i) and final (D_f) tuber densities was ascribed to part of the initial tuber biomass being buried deep, inaccessible to the swans, and the slope of the regression of D_f on D_i was interpreted as the fraction out of reach of the swans (Nolet et al. 2006b). The current analysis suggests that this positive relationship results from periods with high water, which implies that the final tuber density in Lauwersmeer would be similar in all years, independent of initial tuber density, if water levels would remain low throughout the stopover period.

When considering swan-days S, two models were equally well supported by the data. According to both these models, S increased with initial tuber density D_i, but for a given D_i, swan use was lower when more days with high water levels occurred (i.e., large h). We chose to depict the second most parsimonious model (Fig. 4a), because it was biologically the most plausible (the most parsimonious model predicted $S > 0$ at $D_i < 0$), and because it was in line with the most parsimonious model for D_f. This can be seen by writing model 1 in Table 1 as $D_f = b_0 + b_2 \times D_{ic} \times h$, and express it as consumption $C = D_{ic} - D_f = D_{ic} - (b_0 + b_2 \times D_{ic} \times h) = -b_0 + D_{ic} - b_2 \times D_{ic} \times h$. This is very similar in structure as model 2 in Table 2: $S = b_0 + b_1 \times D_{ic} + b_2 \times D_{ic} \times h$.

The results of the analyses of final tuber density and swan-days were therefore in line with each other, and suggest that swans left Lauwersmeer earlier when they encountered high water, leading to an underuse of the stopover site.

The high water levels reduce food accessibility and hence fuelling rate, and induce the birds to continue migration, in accordance with the hypothesis of time-minimizing migration. The reduction in tuber biomass from November to March was as expected from winter mortality from other causes than swan predation, as measured in winter exclosures, confirming that there was no measurable swan foraging after our final sampling in November. Only in 1996 did the relatively large reduction in tuber biomass between November and March of the following calendar year suggest that the swans returned to forage on the lake when water level had returned to normal. This may be because in that year the water levels dropped to normal again relatively early in autumn (on 9 November 1996, only 2 days after our final sampling, 5,000 Bewick's Swans were counted in Lauwersmeer, http://www.waarneming.nl). In a way, this exception proves our concept of underuse, because apparently there was food left to be used by swans.

Tuber loss due to other causes than swan predation is small over the short exploitation period (3 % per month in winter exclosures; Hidding et al. 2009). Hence, the difference between the initial and final tuber density should roughly equal the consumption C by the swans, and the observed patterns of depletion and stopover duration should be reproducible from the functional response of swans feeding on tubers (Nolet et al. 2006b). This functional response model indeed yields very similar patterns as the statistical models, both for D_f (cf. Fig. 3a, b) and for S (cf. Fig. 4a, b). Apparently, local environmental conditions (initial tuber density D_i and days with above average water levels h) largely explain the annual variation in final tuber density D_f and swan-days S.

A rise in bird-days can be due to more birds stopping over at the site or to an increase in stopover duration of individual birds. Whereas there are some indications that staging numbers vary annually with food density at a stopover site (Van Gils et al. 2005), evidence for longer stopover durations at the individual level when resources are plentiful is scarce. In fact, in hummingbirds, the

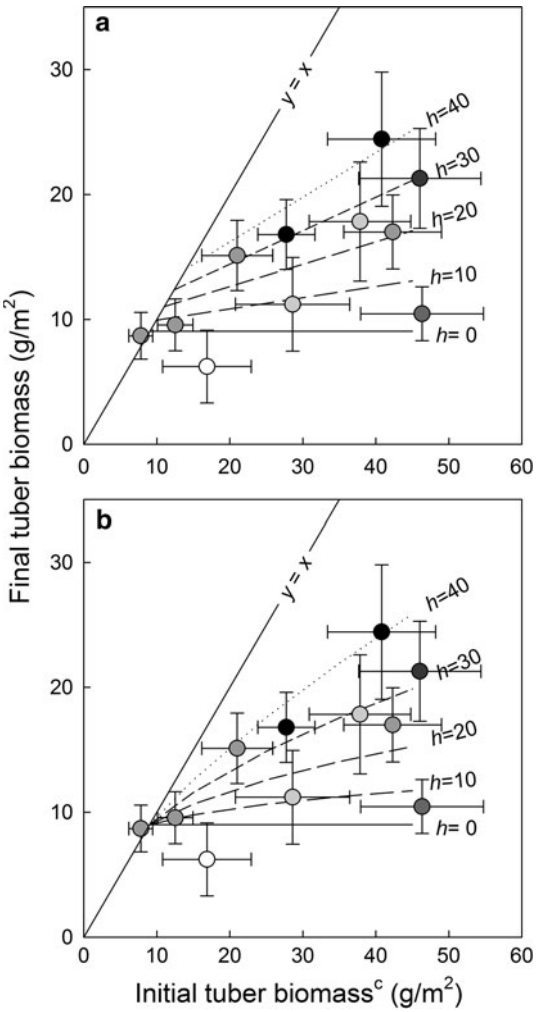

Fig. 3 Final tuber biomass density D_f as a function of corrected initial tuber biomass density D_{ic} and the number of days with high water in Lauwersmeer (h, days). Each data point represents 1 year in the period 1995–2008, with *grey shading* according to h values (from *white* if $h \leq 6$ to *black* if $h > 30$). The difference from a data point to the $y = x$ line along the vertical equals the consumption (g/m^2) by swans. *Error bars* indicate 95 % CI. *Lines* depict **a** most parsimonious model with D_{ic} and h as explanatory variables (model 1 in Table 1); **b** predictions based on linear functional response (see "Methods" for calculation). When there is no restriction by high water levels ($h = 0$), the best statistical model (Table 1, model 1) predicts a final tuber density $D_f(0) = 9.0$ g/m^2

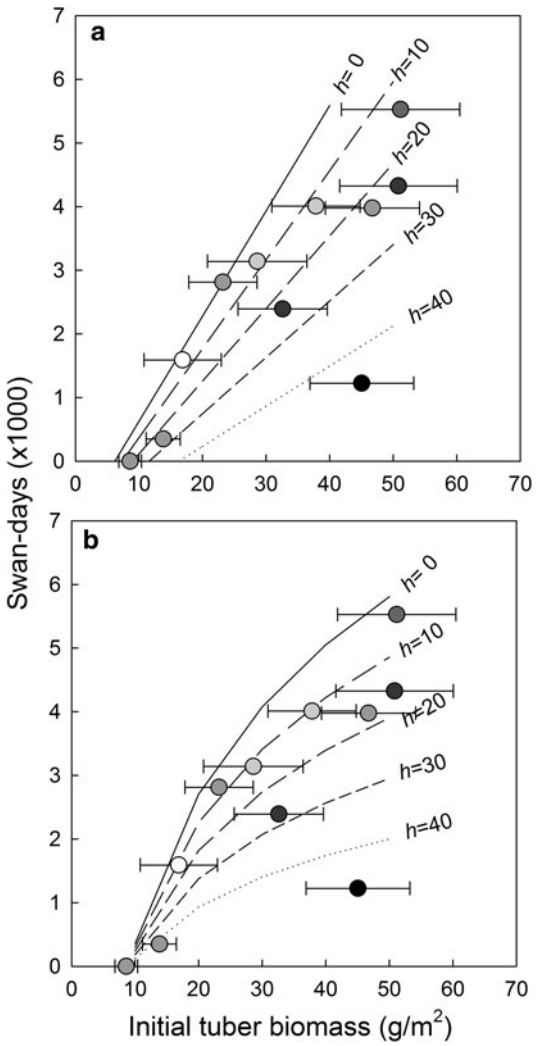

Fig. 4 Swan-days S as a function of initial tuber biomass density D_i and the number of days with high water in Lauwersmeer (h, days). Each data point represents 1 year in the period 1995–2008, with *grey shading* according to h values (see Fig. 3). *Error bars* indicate 95 % CI. *Lines* depict **a** second most parsimonious model with D_{ic} and h as explanatory variables (model 2 in Table 2); **b** predictions based on linear functional response (see Fig. 3 and "Methods" for calculation)

opposite pattern was found, with stopover duration decreasing with resource (i.e., flower) density (Russell et al. 1994). On the other hand, when resource conditions are very poor, birds are found to move on quickly (Newton 2006). Hence, stopover duration may have a humped-shape relationship with resource density: at low resource density, birds leave quickly or skip the site altogether; at intermediate resource density, birds make use of the site but need time to refuel; whereas at high resource density, birds stay

Table 2 Top 3 explanatory models for swan-days S in Lauwersmeer in 1995–2008 according to Akaike's information criterion corrected for small sample size (AICc; $n = 11$). See also Table 1

Model	K	Deviance ratio	ΔAICc	$L(m_i\|x)$	w_i	Evidence ratio	RMSD ($\times 10^3$)	r^2
1. $\boldsymbol{D_i + h}$	**4**	**0.59**	**0.00**	**1.00**	**0.53**	**1.0**	**0.65**	**0.85**
2. $\boldsymbol{D_i + D_i \times h}$	**4**	**0.60**	**0.61**	**0.74**	**0.39**	**1.4**	**0.66**	**0.84**
3. D_i	3	1.25	4.33	0.11	0.06	8.7	1.01	0.63

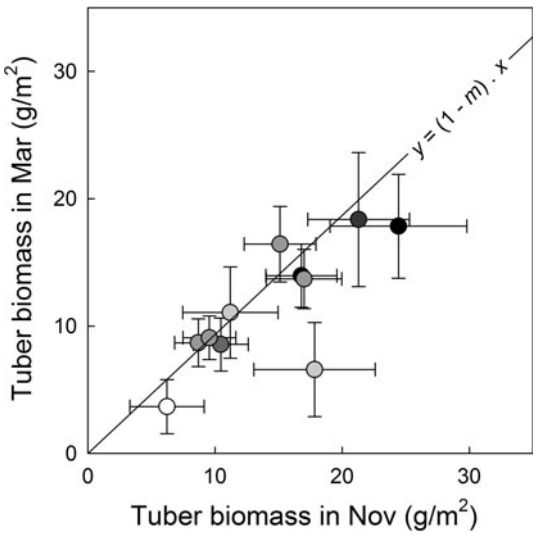

Fig. 5 Final tuber biomass densities in November (after the swans had left the lake) and March of the following calendar year (at the end of the winter). Each point represents 1 year in the period 1995–2008, with *grey shading* according to *h* values (see Fig. 3). *Error bars* indicate 95 % CI. Observed tuber biomass densities in March are generally as expected from the winter mortality (*m*) measured in winter exclosures (*line*, see text)

relatively short periods because they are able to rapidly replenish their stores (Schaub et al. 2008). However, birds are predicted to leave a rich site with relatively high fuel loads, which may extend the fuelling period at rich resource densities despite the more rapid fuelling (Lindström and Alerstam 1992; Klaassen and Lindström 1996). So, the increase in swan-days with resource availability is possibly a combination of more swans stopping over and a net increase in stopover duration per swan. Unfortunately, too few marked swans were available to estimate turnover, especially in the later years, to distinguish between these two possibilities.

A carry-over effect may cause individuals to stage longer at a site when conditions at the previous site were poor (Bauer et al. 2006). Lower fuelling rates are predicted to lead to lower departure fuel loads (Lindström and Alerstam 1992). Therefore, birds are predicted to arrive relatively lean to a next stopover site, which may cause the birds to stay longer there and, in case of depletable resources, deplete these further. Some studies indeed have shown that lean arriving migrants generally stayed longer than fat ones (Cherry 1982; Bairlein 1985; Biebach et al. 1986; Moore and Kerlinger 1987; Goymann et al. 2010), or that stopover duration was longer when in a given year body condition at arrival at the stopover site was low (Russell et al. 1994). However, some other studies have found no consistent relationship between arrival condition and stopover duration (Safriel and Lavee 1988; Butler et al. 1997; Skagen and Knopf 1994; Lyons and Haig 1995; Holmgren et al. 1993), possibly because departure was triggered more by time schedules or flight conditions (e.g. favourable weather) than by fuelling conditions. The large variation in giving-up tuber densities and swan-days explained by local effects of food density and accessibility, as well as the close fit with the functional response model, suggests that such carry-over effects were small in comparison to local effects.

Our study provides clear evidence for underuse of a stopover site, in line with time-minimizing migration. Underuse of stopovers has been reported before, but in those cases it was used in the sense that migratory birds leave more food at stopover sites than at wintering sites because on the latter they should reflect energy balance rather than a positive energy budget (Van Eerden et al. 1997a; but see Lourenço et al. 2010; Alonso et al. 1994). Here, we show that migratory birds may also underuse a stopover site in the sense that they leave more food behind in some years than in others, because of yearly differences in fuelling conditions.

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